

Food consumption by Collembola from northern Michigan deciduous forest¹

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Summary. The present study was designed to assess food partitioning mechanisms in Collembola. *Isotoma notabilis*, *Sminthurinus henshawi* and *Orchesella hexfasciata* were dominant litter-dwelling Collembola in northern Michigan deciduous forests. Little overlap in mouthpart size occurred between species. *Isotoma notabilis* had the shortest mandible and labrum, *O. hexfasciata* the longest, whereas *S. henshawi* was intermediate. Gut content analysis showed that these species fed on different food types and selected different size food particles. Selection of food particle size was related to mouthpart size. Gut contents were categorized as fungal hyphae and spores, plant material and pollen, animal remains, colloidal materials, minerals and bacteria. Fungal hyphae and colloidal material were most abundant in the gut of *I. notabilis*, while *S. henshawi* fed heavily on fungal spores, and *O. hexfasciata* incorporated diversified foods in its diet. Type and size of food ingested were found to be species-specific. All species showed variation in dietary components related to seasonal availability of foods in the field.

Key words: Collembola, mouthparts, gut contents, food type, food particle size

Introduction

Collembola are numerically dominant microarthropods living in litter and soil. They can feed on a wide range of foods. Fungal hyphae and spores, plant material, algae, diatoms, amorphous material, arthropod feces and exuvia are major food components found in the intestines of field-collected individuals (Poole 1959; Bödvarsson 1970; Knight 1976). The diets of most co-existing species do not differ as much as those of single species living in different habitats (Gilmore & Raffensperger 1970). There is generally less evidence for food differentiation in co-existing Collembola when compared to other invertebrate herbivores (Anderson & Healey 1972; McMillan 1975; Takeda & Ichimura 1983).

Size of individual particles consumed could be as important in niche segregation as type of particles ingested (Cummins 1973). Most gut content analyses have concentrated on types of collembolan foods; very few studies have mentioned food particle size differentiation between species (Anderson & Healey 1972; McMillan 1975).

Feeding habits are closely related to mouthpart structure. Collembola use their mouthparts to manipulate food items during the feeding process. Movement of mandibles and maxilla is small because of restriction by surrounding structures, such as labrum, labium and the

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lateral margins of the gnathal pouch (Manton 1964). Size and structure of mouthparts may restrict type and particle size of food ingested by Collembola (Fjellberg 1985), and therefore may contribute to niche separation through their feeding habits.

The present study was designed to assess the relationship between mouthparts and food (particle size and type) of co-existing litter Collembola collected from a deciduous forest floor. Effects of seasonal environmental conditions on gut contents were also investigated.

Materials and Methods

Site description

Collembola observed in this study came from the Test and Control sites used for soil biological studies (ELF ecological monitoring project) in 1988 and 1990. These two sites were closely matched with respect to physical and chemical characteristics (Snider & Snider 1987). The "Test" site of Project ELF will be referred to as Site I and the "Control" as Site II in the present study. Both sites are located in Dickinson County, Upper Peninsula, Michigan. Detailed descriptions of the study areas are given in Snider & Snider (1987).

The general area climate is temperate continental of the cool summer type. Air temperatures near the forest floor were virtually the same in both sites. Both sites were secondary growth deciduous forests, dominated by maple (*Acer saccharum* Marsh), with basswood (*Tilia americana* L.) subdominant. Pine trees were located in areas adjacent to both sites. Annual leaf litter inputs in both sites were approximately equal. Leaf abscission generally peaked in early October.

Source of specimens

Site I and II were each divided into 20 (10 × 10 m) quadrats, from which samples were obtained periodically. Collembola used for gut content analysis stemmed from two types of samples:

a) Pitfall traps: each quadrat contained a permanently installed pit-trap, with ethylene glycol as the collecting medium. After samples were gathered, they were washed into 95% ethanol and stored until further treatment.

b) Leaf litter samples: litter samples (25 × 25 cm) were randomly collected from ten quadrats on the forest floor at two week interval. The samples were then placed in Tullgren funnels fitted with 40 watt bulbs, for about eight days to extract animals. Animals were collected in jars containing 95% ethanol.

Selection of species

More than 30 collembolan species were collected from both sites. Three species were chosen for this study: *Isotoma* (*Desoria*) *notabilis* Schaeffer (extracted from leaf litter), *Sminthurinus* (*Sminthurinus*) *henshawi* (Folsom) and *Orchesella hexfasciata* Harvey (both obtained from pit-traps). They were selected because of their relatively high dominance in both sites, and because of their consistent occurrence from May to October. *Isotoma notabilis* represented 56% of all Collembola in litter samples from Site I and 62% of those from Site II. *Sminthurinus henshawi* represented 30% and *O. hexfasciata* 26% of all Collembola captured in pitfall traps in 1988, and 21% of the total in 1990 were *O. hexfasciata* (Snider & Snider 1990, 1992). Only adult specimens were used in this study.

Interspecific, within-year comparisons were based on 1988 data for all three species. In the case of *O. hexfasciata*, 1988 and 1990 data were used for between-year intraspecific analyses.

Analyses of seasonal differences were based on samples obtained at intervals ranging from two to five weeks. Although pit-trap samples were available at weekly, and litter samples at biweekly intervals, only samples with sufficient numbers of individuals from both sites were used here (for a total of seven or eight dates per year). In the subsequent presentation of results, "Week 1" through "Week 24" will span a time period from early May through mid-October.

Sample preparation and analyses

Before dissection, head and trunk length of each individual were recorded. Mandibles and maxillae were separated from the head capsules and mounted in a small drop of Hoyer's medium (Borror et al. 1976) on a glass slide. Total length of the mandible was measured under a phase-contrast microscope. Mandibles and maxillae were examined for their detailed structure. Labra were at first discarded, but were later included in the study. Dissection of an additional set of specimens showed that labrum width could be reliably estimated by regression ($R^2 > 0.95$) based on head, trunk and mandible length.

Gut contents of individual specimens were dissected, dispersed in Canada Balsam on a glass slide, and examined under a phase-contrast microscope at $750\times$ magnification. Eight food categories were identified as follows: fungal hyphae, fungal spores, plant materials, pollen, animal remains, minerals, bacteria and colloidal material. A small portion of the gut contents could not be identified based on current knowledge and was placed into an "unknown" category. Each food category was measured using a grid eye-piece and the data were converted to percentages for each specimen. Among several transformations, only square root yielded homogeneous variance to treatment groups for most food categories. All data were transformed by square root before analysis. Pollen was further separated into pine pollen and non-pine pollen. Relative percentages of pine and non-pine pollen were calculated based on the total pollen amount, and nonparametric statistics were used to analyze pollen data. Detailed gut content records were based on a total of 858 specimens (204 specimens of *I. notabilis*, 234 *S. henshawi*, 203 *O. hexfasciata* in 1988 and 217 in 1990).

For each individual, approximately 100 food particles, randomly chosen, were measured for their two-dimensional size and grouped into three (small, medium and large) size classes. Small corresponded to particles smaller than $6\mu\text{m}^2$, medium particles measured between 6 and $20\mu\text{m}^2$, and large ones were $>20\mu\text{m}^2$. The raw data were converted to percentages (p) and then transformed by $\log_e [p/(1 - p)]$ to achieve homogeneous variance before statistical analysis.

Results

Mouthparts

These three species all possessed chewing type mouthparts, i.e., their mandibles were provided with a well-developed molar plate in addition to apical teeth. The general shapes of mandibles, maxillae and labrum were very similar (Chen et al., in press).

Mandible length differed between species. *Isotoma notabilis* had the shortest, ranging from 81 to $130\mu\text{m}$ with more than 90% of samples shorter than $120\mu\text{m}$. Mandible size of

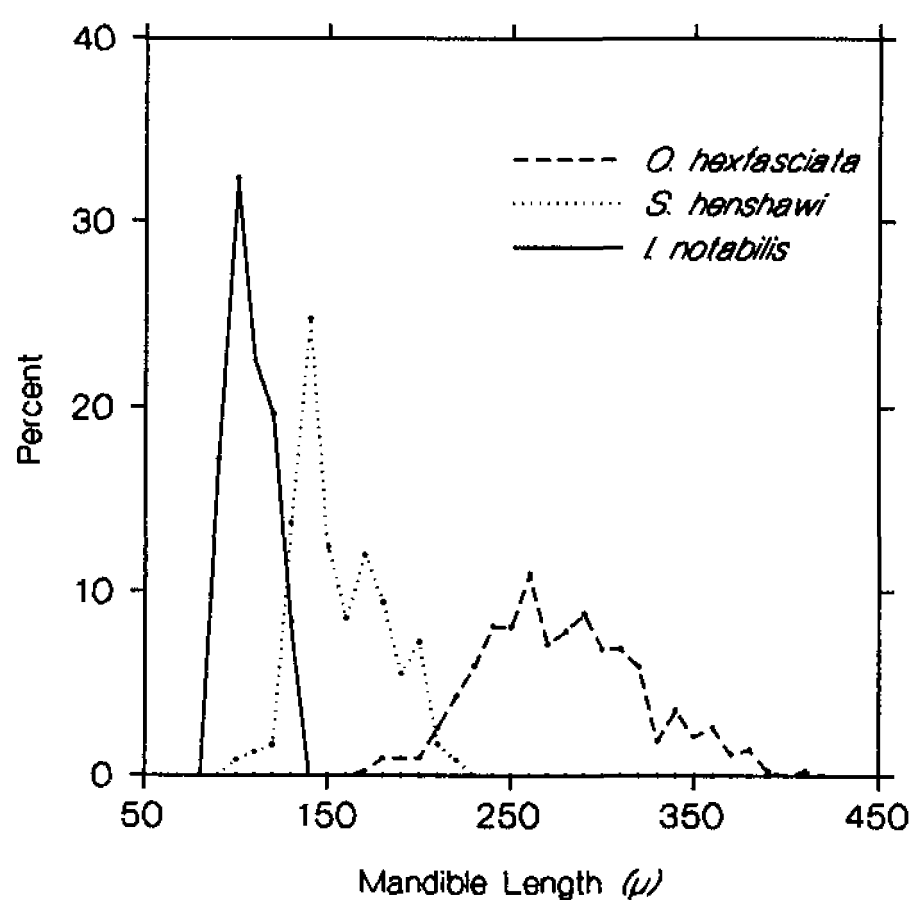


Fig. 1. Mandible length frequency distribution of three collembolan species

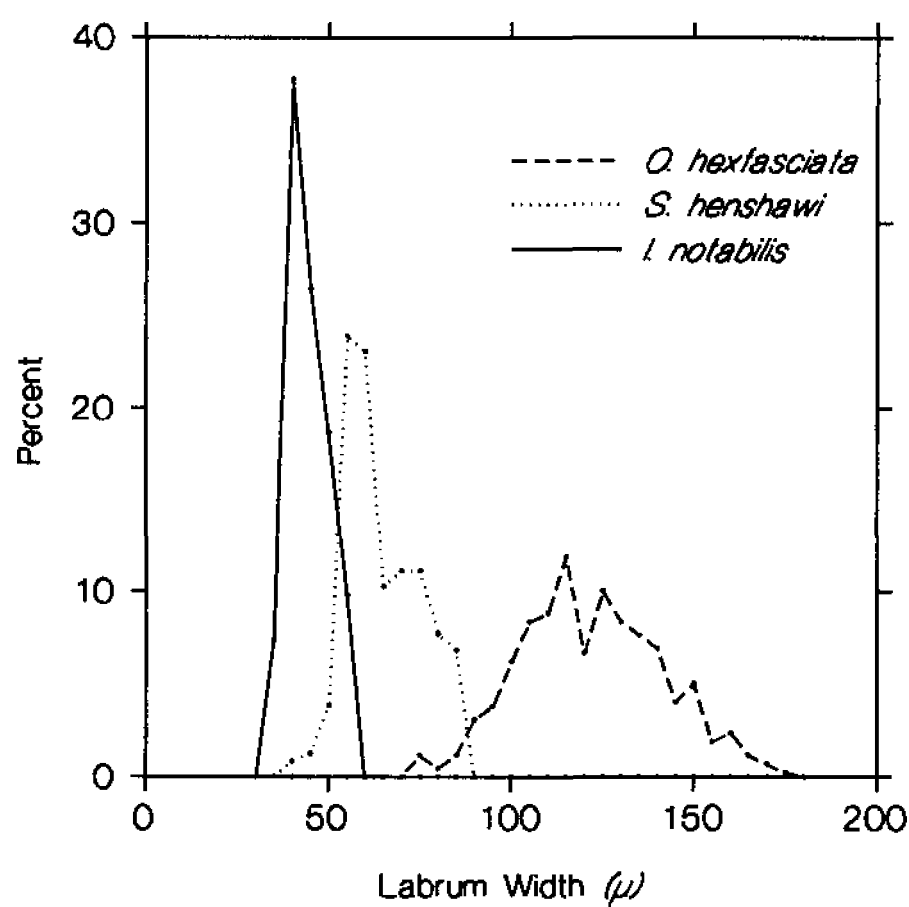


Fig. 2. Labrum width frequency distribution of three collembolan species

S. henshawi was intermediate, ranging from 92 to 216 μm with more than 90% in the range of 120 to 200 μm . *Orchesella hexfasciata* had the longest, in the range of 164 to 403 μm with more than 95% longer than 200 μm . There was very little interspecific overlap in mandible length (Fig. 1). Although some minor anatomical differences were observed between species, it is difficult to explain how these differences would affect feeding habits. On the other hand, mandible size differences suggested some differences in feeding habits (especially the size of food particles that they can handle) among species.

The estimated labral width of *I. notabilis* ranged from 31 to 55 μm with 90% shorter than 50 μm ; 37 to 90 μm with more than 94% between 50 to 90 μm in *S. henshawi*; and 71 to 171 μm with more than 94% wider than 90 μm in *O. hexfasciata*. There was very little overlap in labral width among the three species (Fig. 2). Again, it is difficult to relate minor structural differences to the species' food habits. The maximal mouth opening is limited by labrum, and labral width which may, therefore, determine the size range of particles on which each species can forage.

Food particle size distribution

Large particle size range differed between species. In *I. notabilis*, most large particles were in the range of 44 to 110 μm^2 with very few larger than 110 μm^2 . The majority of large particles found in *S. henshawi*'s guts ranged from 44 to 180 μm^2 , and the largest was approximately 820 μm^2 . *Orchesella hexfasciata* contained relatively evenly distributed large particles from 44 to 360 μm^2 with some extremes reaching 3600 μm^2 .

It is clear that *I. notabilis* ate a high percentage of small and medium (both more than 40%), and a very low percentage of large particles (less than 15%) (Fig. 3). The three size categories' distribution was relatively even for *S. henshawi*, with medium size particles only slightly more frequent (40%) than the other two. *Orchesella hexfasciata* contained a very low percentage of small particles (less than 20%) and a very high percentage of large particles (more than 45%) (Fig. 3).

Seasonal variations in particle size distribution in each site are illustrated for *I. notabilis* (Fig. 4), for *S. henshawi* (Fig. 5), for *O. hexfasciata* (1988) (Fig. 6) and for *O. hexfasciata* (1990) (Fig. 7). *Isotoma notabilis* always contained a very low percentage of large particles (less than 15% except Week 1), and small and medium sizes usually ranged from 40–50% each. In most cases, each of the three size categories constituted 20–45% of the total in *S. henshawi*, with medium size particles most prominent. For *O. hexfasciata*, the percentage of large particles was always higher than 40%, sometimes near 60%, and small particles were infrequent (usually less than 20%).

Multivariate analysis of variance was used to test differences between the species in 1988 and differences between 1988 and 1990 for *O. hexfasciata*. Results showed highly significant differences between species and between weeks. Separate analyses of variance for each

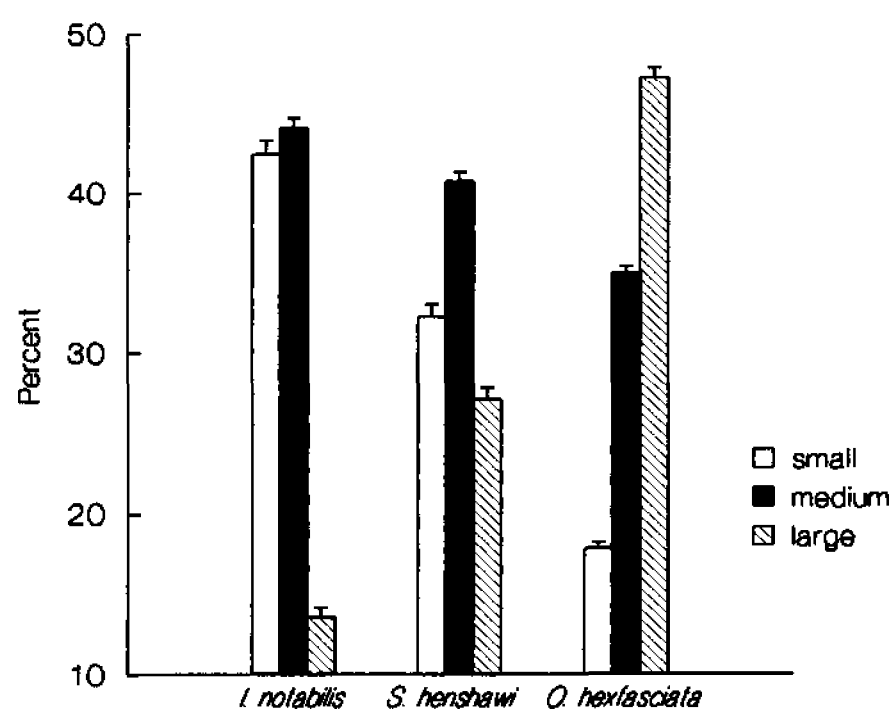


Fig. 3. Average food particle size (Mean $\pm$ SE) distribution in three collembolan species. Small: $< 6 \mu\text{m}^2$. Medium: 6 to 20 μm^2 . Large: $> 20 \mu\text{m}^2$

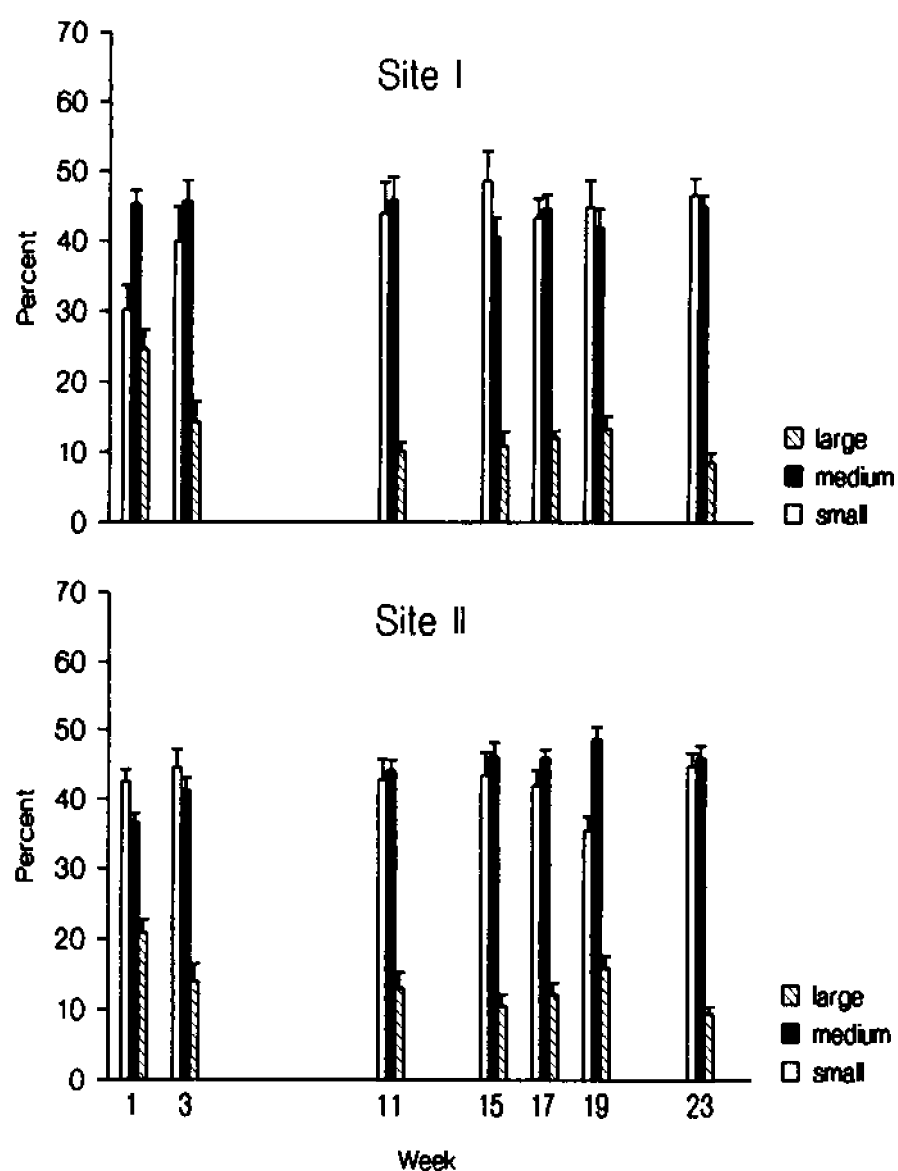


Fig. 4. Seasonal food particle size (Mean $\pm$ SE) distribution in *I. notabilis*

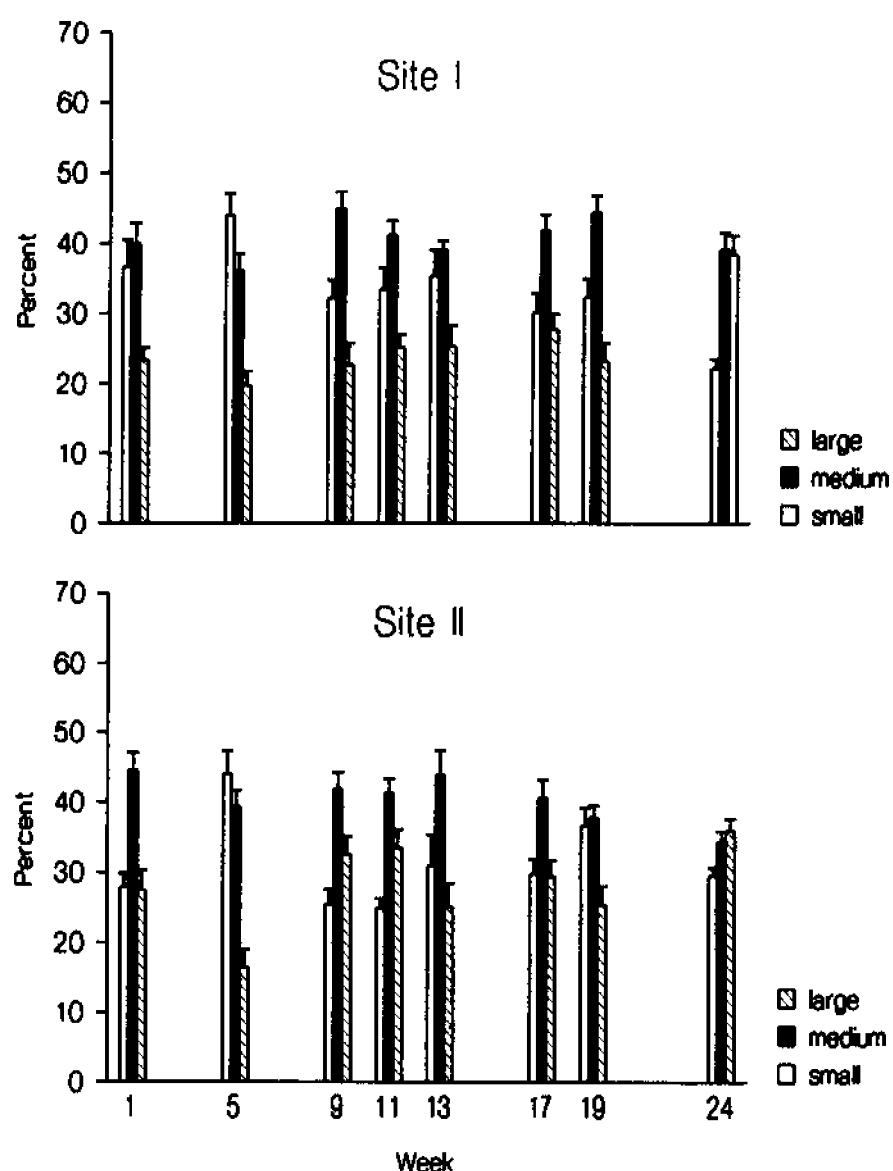


Fig. 5. Seasonal food particle size (Mean $\pm$ SE) distribution in *S. henshawi*

species and year revealed that there were no average differences between sites for either *I. notabilis* or *S. henshawi*; however, significant interactions suggested that particle size distribution underwent different seasonal changes in the two sites. In *O. hexfasciata*, particle size distribution did not differ between years, and there were no site effects in either 1988 or 1990.

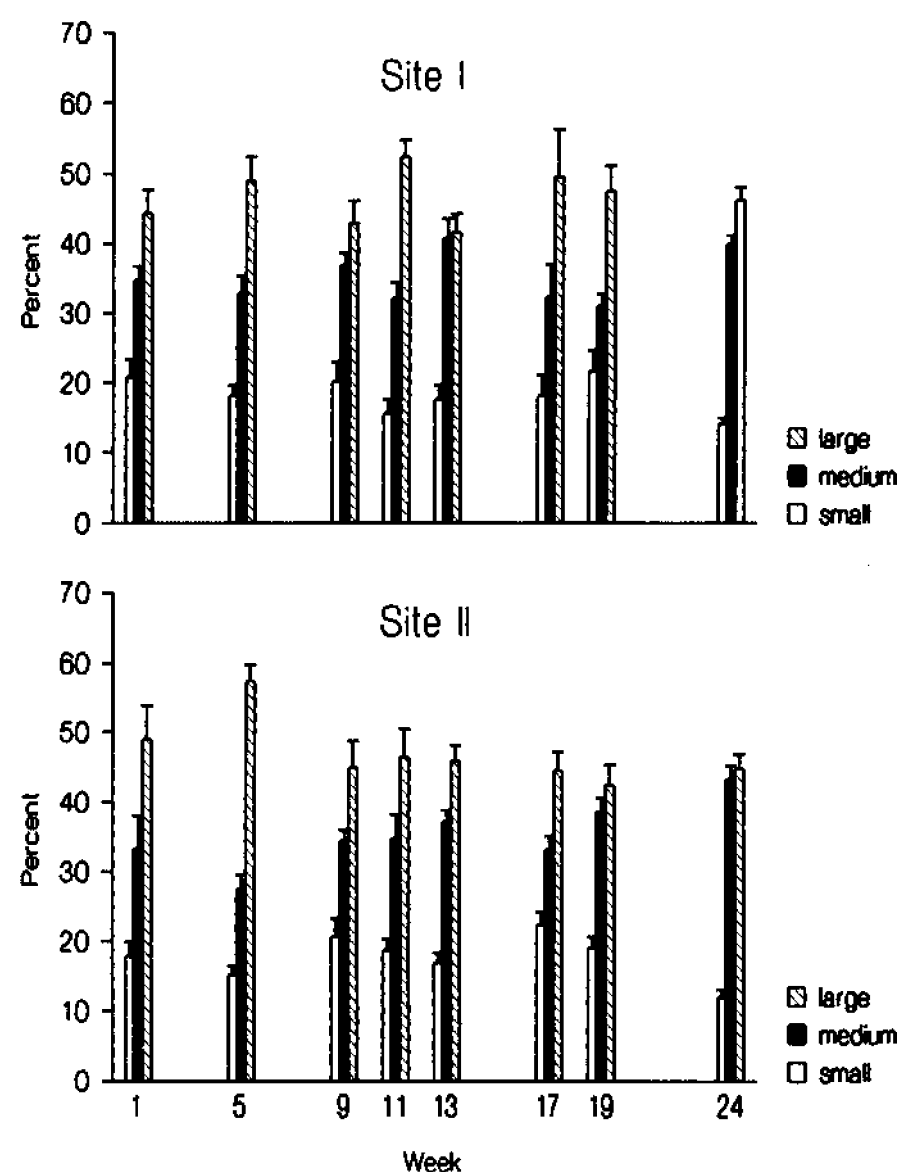


Fig. 6. Seasonal food particle size (Mean $\pm$ SE) distribution in *O. hexfasciata*, 1988

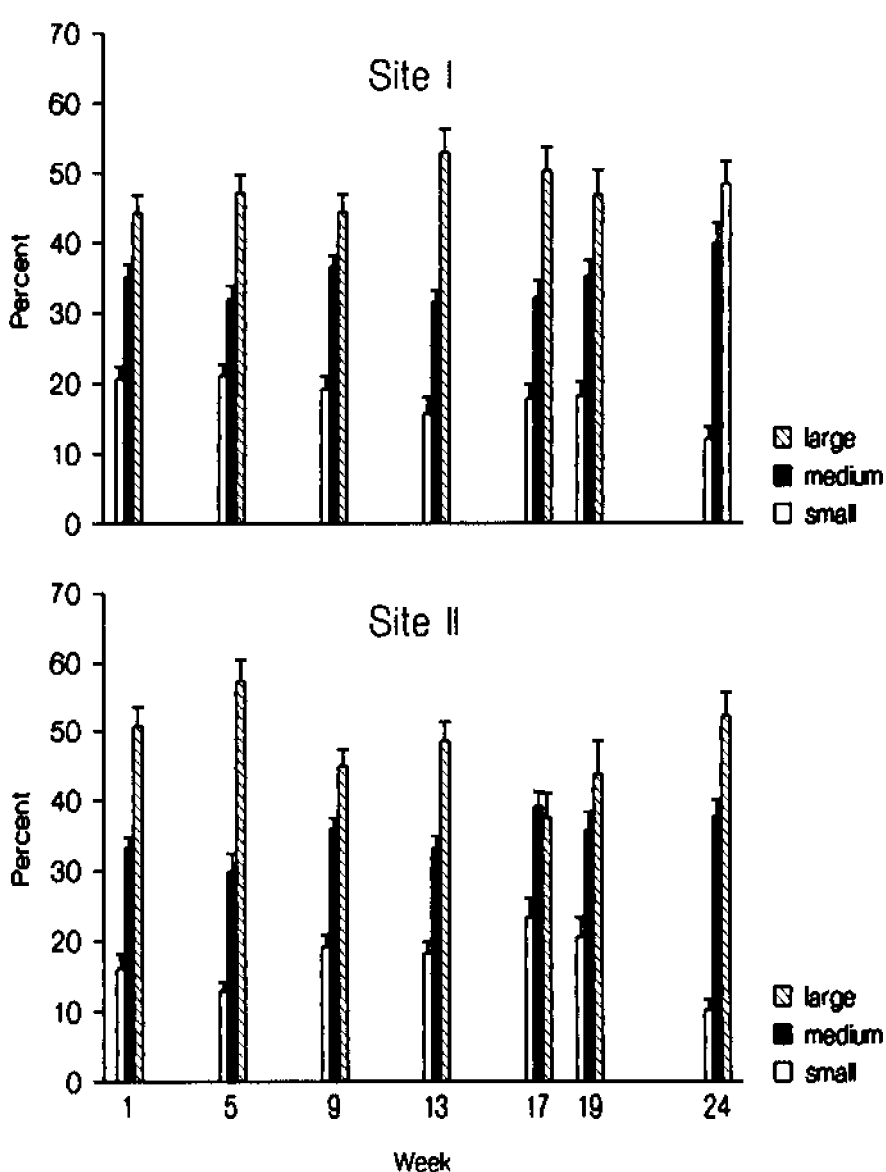


Fig. 7. Seasonal food particle size (Mean $\pm$ SE) distribution in *O. hexfasciata*, 1990

Food components

There were general similarities between species: fungal hyphae and spores, plant materials and colloidal materials made up the majority of gut contents (Table 1). On average, more than 95% of gut contents of *I. notabilis* and *S. henshawi*, and more than 80% of these in *O. hexfasciata* consisted of these four food items.

There were also striking differences between species: in each the major food items appeared in different proportions. Colloidal materials and fungal hyphae were the dominant foods in the gut of *I. notabilis*. In *S. henshawi* and *O. hexfasciata*, fungal spores were most frequent. Pollen was another important food item for *O. hexfasciata*, especially in 1988 (Table 1).

Most plant materials found were brown, unstructured and humus-like substances. Only a few *O. hexfasciata* contained litter remains of higher plants. Colloidal materials were mostly of unknown origin. They could have been partially digested food, or may have been in a liquid state before ingestion.

Isotoma notabilis had the most restricted or specialized diet. It did not feed on pollen, animal remains, or bacteria. *Sminthurinus henshawi* did feed on pollen and animal remains, but animal remains were found in only two specimens. *Orchesella hexfasciata* had the most varied diet.

There were highly significant interspecific differences with respect to all food categories except bacteria. Site effects (across all species) were never significant. Seasonality (week effect) was strong for all major food items except for colloidal materials.

Most of the pollen encountered in *O. hexfasciata* was pine pollen, whereas more than 2/3 of the pollen found in *S. henshawi* was non-pine pollen (Table 2). Statistical analysis

Table 1. Percent (Mean $\pm$ SE) of dietary components in the guts of three collembolans. (No. = total number of specimens examined; Hyph. = fungal hyphae; Spor. = fungal spores; Pl. Ma. = plant material; Poll. = pollen; Anim. = animal remains; Co. Ma. = colloidal material; Mine. = minerals; Bact. = bacteria; Unkn. = unidentifiable material; NP = none present; * = less than 1)

Species	Site/ Year	No.	Hyph.	Spor.	Pl. Ma.	Poll.	Anim.	Co. Ma.	Mine.	Bact.	Unkn
<i>I. notabilis</i>	I/88	99	31 $\pm$ 2	9 $\pm$ 1	10 $\pm$ 1	NP	NP	45 $\pm$ 2	* $\pm$ *	NP	5 $\pm$ 1
	II/88	105	35 $\pm$ 2	7 $\pm$ 1	11 $\pm$ 1	NP	NP	45 $\pm$ 1	* $\pm$ *	NP	2 $\pm$ *
<i>S. henshawi</i>	I/88	118	14 $\pm$ 1	37 $\pm$ 2	17 $\pm$ 1	3 $\pm$ 1	NP	28 $\pm$ 1	1 $\pm$ *	NP	* $\pm$ *
	II/88	116	11 $\pm$ 1	42 $\pm$ 2	12 $\pm$ 1	1 $\pm$ 1	* $\pm$ *	30 $\pm$ 2	1 $\pm$ *	NP	1 $\pm$ *
<i>O. hexfasciata</i>	I/88	101	7 $\pm$ 1	29 $\pm$ 3	17 $\pm$ 2	13 $\pm$ 2	4 $\pm$ 1	23 $\pm$ 2	1 $\pm$ *	1 $\pm$ 1	4 $\pm$ 1
	II/88	102	8 $\pm$ 1	30 $\pm$ 3	20 $\pm$ 2	10 $\pm$ 2	3 $\pm$ 1	22 $\pm$ 2	1 $\pm$ *	NP	6 $\pm$ 1
	I/90	109	8 $\pm$ 1	28 $\pm$ 2	27 $\pm$ 2	4 $\pm$ 1	6 $\pm$ 2	21 $\pm$ 1	1 $\pm$ *	* $\pm$ *	6 $\pm$ 1
	II/90	108	6 $\pm$ 1	31 $\pm$ 2	26 $\pm$ 2	5 $\pm$ 1	3 $\pm$ 1	24 $\pm$ 1	1 $\pm$ *	NP	3 $\pm$ *

Table 2. Relative percentage (based on the total amount of pollen) of pine and non-pine pollen found in the guts of *S. henshawi* and *O. hexfasciata*

Species	Site/Year	Pine pollen	Non-pine pollen
<i>S. henshawi</i>	I/88	32.2	67.8
	II/88	26.9	73.1
<i>O. hexfasciata</i>	I/88	90.5	9.5
	II/88	94.5	5.5
	I/90	91.6	8.4
	II/90	93.2	6.8

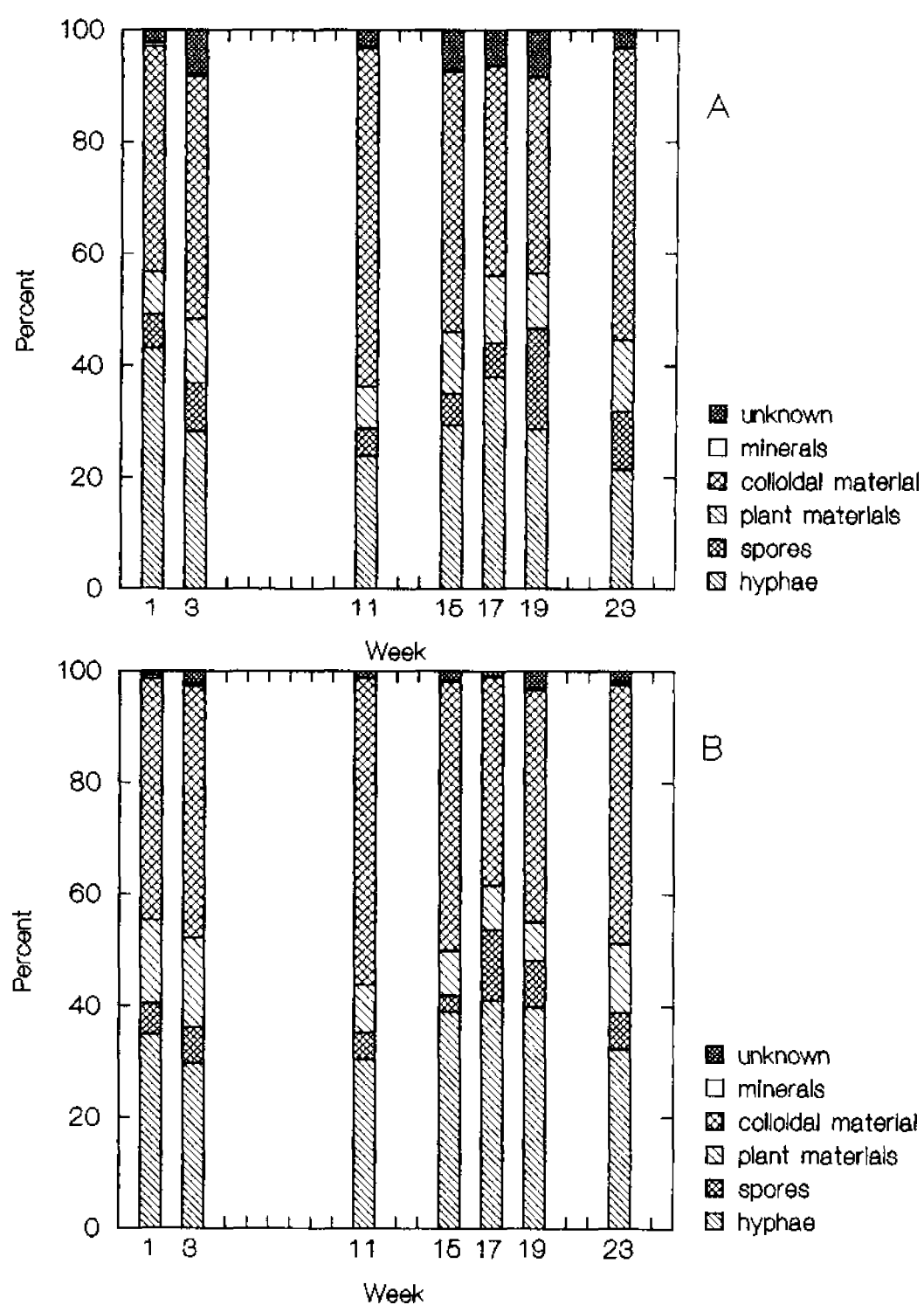


Fig. 8. Seasonal food components of *I. notabilis*. A: Site I. B: Site II

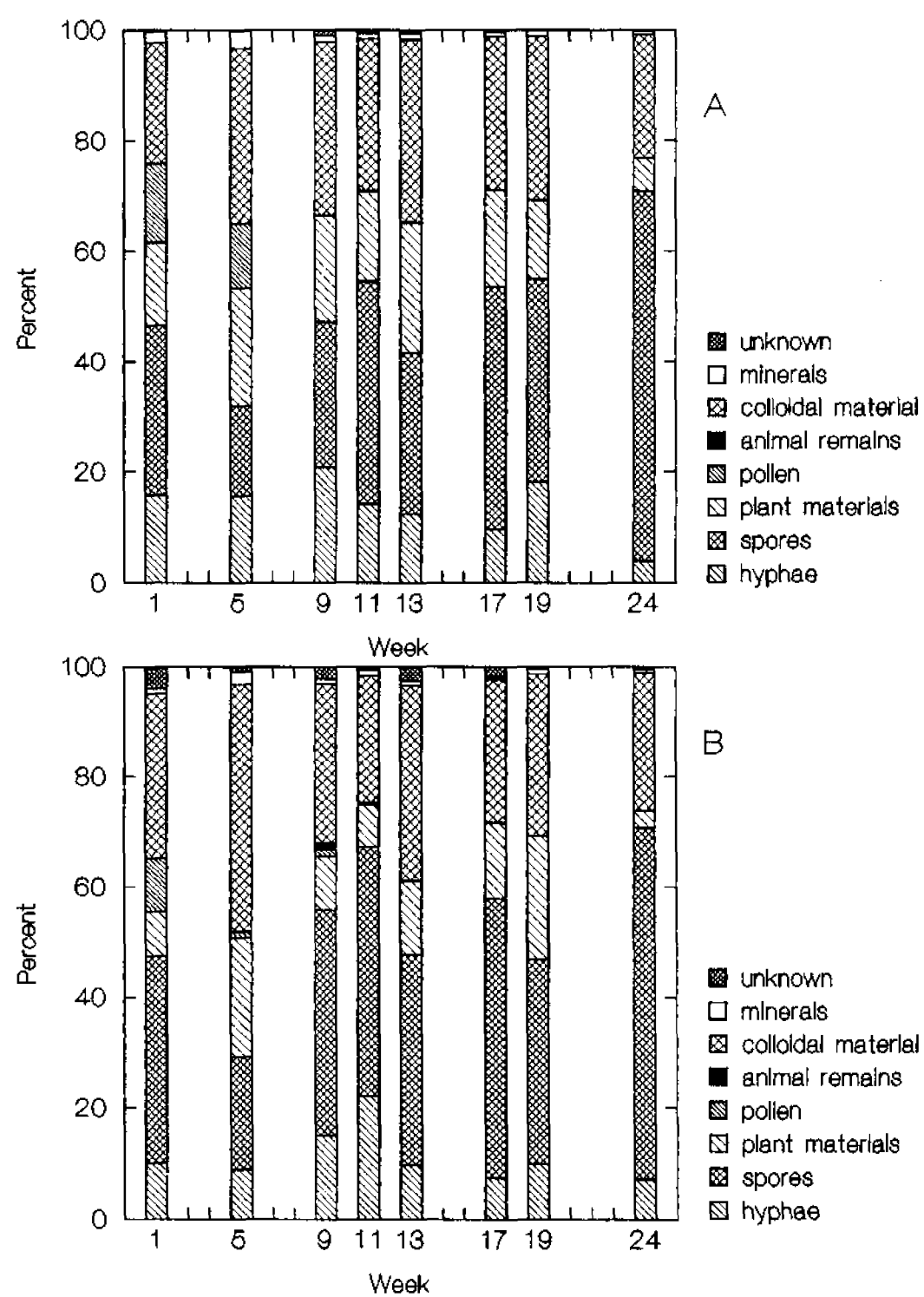


Fig. 9. Seasonal food components of *S. henshawi*. A: Site I. B: Site II

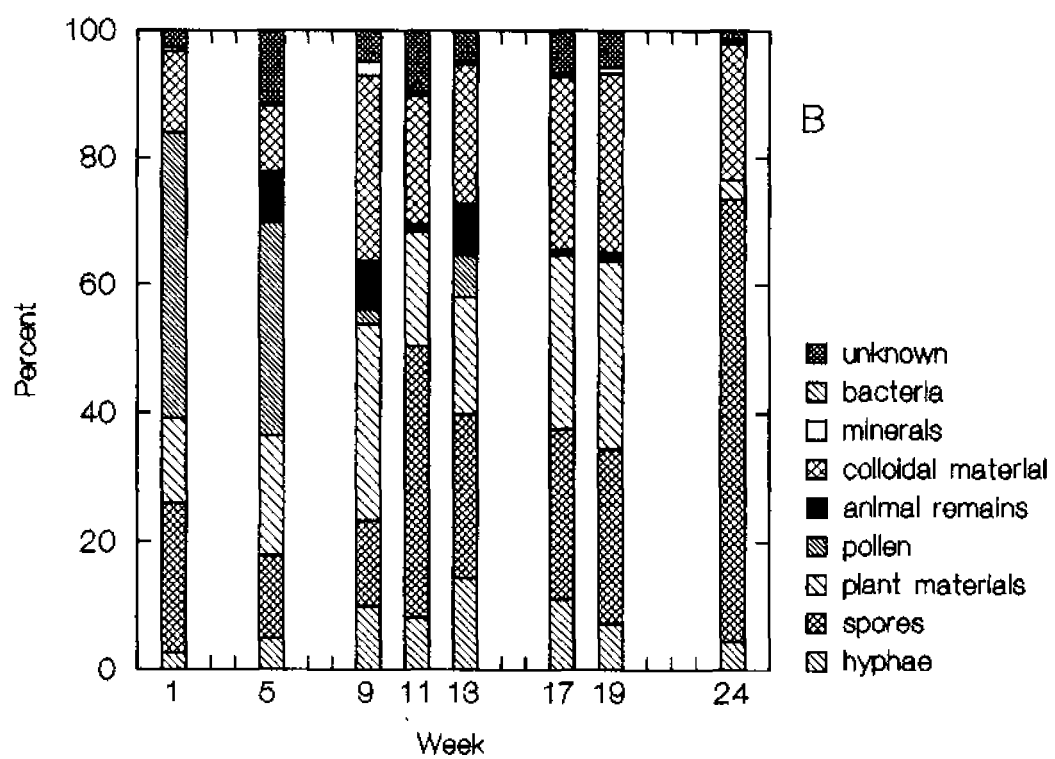
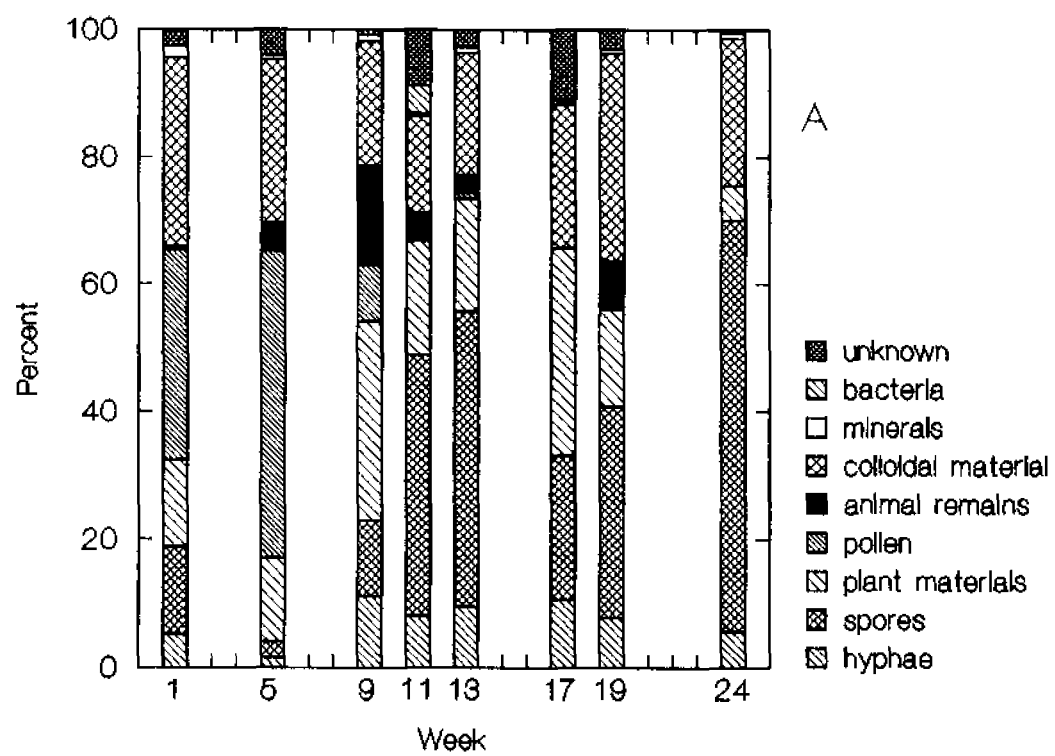


Fig. 10. Seasonal food components of *O. hexfasciata*, 1988. A: Site I. B: Site II

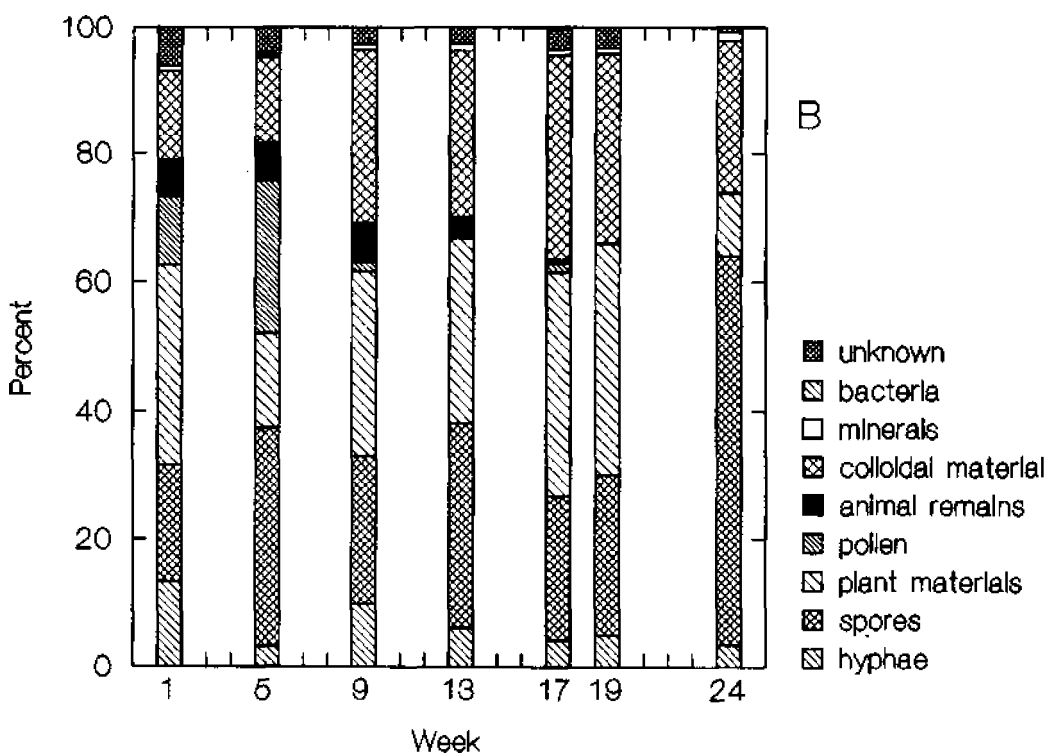
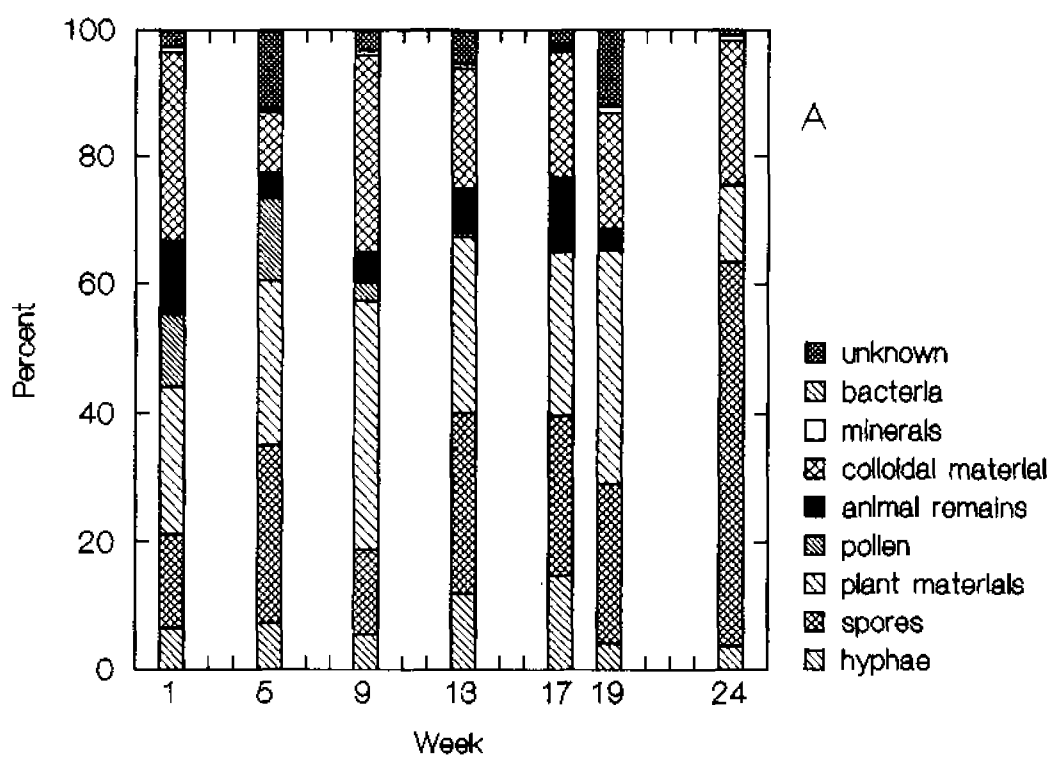


Fig. 11. Seasonal food components of *O. hexfasciata*, 1990. A: Site I. B: Site II

confirmed that these two species consumed pine and non-pine pollen in different proportions, and that there was no site difference for either species.

Analysis of data for *O. hexfasciata* revealed that fungal hyphae, colloidal materials and animal remains were very constant food items in 1988 as well as 1990. However, specimens from 1988 contained significantly more pollen and less plant material than those from 1990. There was no difference in the proportion of pine and non-pine pollen between 1988 and 1990.

In *I. notabilis*, most food items showed very pronounced seasonal variation, only plant materials being marginally significant (Fig. 8). Compared to the other two species, however, seasonal variations in major food components were relatively moderate in *I. notabilis* (Figs. 8, 9, 10 and 11).

Seasonal (week) effects were also significant for most food items in the guts of *S. henshawi* and *O. hexfasciata*. Fungal spore content increased sharply and plant materials decreased in the last week (Week 24) of the season in both sites (Fig. 9, 10 and 11). Pollen only occurred in spring and early summer. In *O. hexfasciata*, animal remains only accounted for 4% of gut contents on average; in some weeks, however, (e.g., early July in Site I, Week 9 of 1988) they reached 15% of total gut contents (Fig. 10). Mite and collembolan exoskeletons (mainly *O. hexfasciata*'s own cuticles), protozoa and nematodes were found among these animal remains.

Discussion

Joosse & Testerink (1977) reported that Collembola extracted in Tullgren funnels had an extremely low proportion of individuals with food in their guts. In the present study, *I. notabilis* extracted in Tullgren funnels yielded a reasonable number (average 69%) of individuals containing food compared to previous work (50–80% with gut contents). The majority of Collembola in a given litter sample were obtained during the first day of extraction (data from a preliminary study). Extraction of all samples was carried out under the same conditions, so that loss of gut contents, if any, should remain relatively constant over different sampling dates. The Tullgren funnel extraction method used here appeared not to have strong effects on variations in gut contents of these individuals.

There is ample evidence from aquatic insect studies that co-existing species consume different foods (Wallace & Merritt 1980). Larvae of three trichopteran species utilized different sizes and types of food to partition their resources (Wallace 1975). Mouthpart structure was found to be closely related to the feeding habits of Diptera larvae (Surtees 1959; Harbach 1977). In a study of soil oribatid mites, Kaneko (1988) concluded that the shape of the chelicerae was related to feeding habits of these mites. Christian (1989) found that co-existing intertidal Collembola equipped with different mouth structures and fed on different food items.

In this study, the three dominant litter-dwelling collembolan species also partitioned their food resource by utilizing different types and sizes of food. Food size partitioning was determined by mouthpart structure of each species: animals with large mandibles and labrum ingested a greater proportion of large particles, animals with medium-sized mandibles and labrum ate a larger proportion of medium-sized particles, and animals with the smallest mandibles and labrum ingested mostly small particles. The largest particles found in these collembolan species were animal cuticles and pollen grains. Both were found only in *S. henshawi* and *O. hexfasciata* but not in *I. notabilis*. Lack of pollen in *I. notabilis* indicates that *I. notabilis* lives in a different microhabitat compared to the other species, and that pollen may be unavailable to it; or that *I. notabilis* does not prefer pollen; or that *I. notabilis* cannot handle pollen because of the small size of its mouthpart structures. The labral width in *I. notabilis* ranges from 31 to 55 μm with 95% of the measurements smaller than 50 μm . The maximal mouth opening for *I. notabilis* is thus less than 50 μm , minus the spaces occupied by mandibles and maxillae. Pine pollen found in the field measured $80 \times 40 \mu\text{m}$, and non-pine pollen measured about 40 μm in diameter. Thus, it is most likely

that *I. notabilis* did not feed on pollen because of size restriction. *Orchesella hexfasciata* had the biggest mandibles and labrum, and its gut also contained the highest proportion of animal cuticles and pollen grains.

These "chewing type" species can use their mandibles to cut food before ingestion, but whether the mandibles have 'grinding' function is still an open question (Goto 1972, Chen et al., in press). Most pollen and fungal spores found in this study and previous studies were intact, non-broken grains. It seems that the animals "swallowed" these grains instead of grinding them during the feeding processes.

The feeding processes could reduce the particle size in the guts compared to the food particle size they foraged on, thus increased the proportion of the smallest particles in the guts. Since the mouthpart structures and feeding processes of these three species are very similar, bias towards the smallest gut particles should be the same to all three species. Future studies should emphasis on food particle size of unbroken materials.

The nature of these small animals forced us to use two dimensional particle area as an indicator for food particle size. The results should be interpreted with caution. Food particles are three dimensional, and the two shortest linear dimensions determine their acceptability to Collembola.

Since the size of mouthparts are closely correlated with their body size, it is obvious that immature individuals have smaller mouthparts. The mouthpart size of immature *O. hexfasciata* will overlap with adult *S. henshawi*, and immature *S. henshawi* overlap with adult *I. notabilis*. They likely would feed on same food particle size with each others. Very few immature *O. hexfasciata* and *S. henshawi* were obtained from our samples. It is also possible that most immatures occurred in seasons different from their adults. There were also twenty more other collembolan species living on the forest floor. These species had relative low densities. Their body size may well overlap with the three species presented in this study, and feed on similar foods.

Presence of different food types does not necessarily mean that the animal derives its nutrition from these items in proportion to their occurrence in the gut. But a close relationship between ingested and assimilated food would be expected from evolutionary processes (Cummins 1973), since ingestion of large quantities of non-assimilable food would represent wasted energy and would reduce the competitive potential of a species.

The method employed in this study has a well-known weakness: it tends to over-emphasize the relative importance of durable, non-digestible materials, and under-estimate the importance of quickly-digested materials. However, gut content analysis is one of the techniques most readily available and widely used for the study of food selection and partitioning.

These three species also partitioned their resources by using different food items. *Isotoma notabilis* fed more heavily on fungal hyphae and colloidal material, *S. henshawi* ingested a greater proportion of fungal spores and *O. hexfasciata* incorporated more diversified foods in its diet. The gut contents of *I. notabilis* in this study agree in general with a previous study (Poole 1959), in which fungal hyphae were found to be a more important component than spores. Although both pine pollen and non-pine pollen were found in *O. hexfasciata* and *S. henshawi*, each species preferred pollen of a different kind.

Increase of spores and decrease of plant materials in the gut of *O. hexfasciata* and *S. henshawi* in late fall could be attributed to increased availability of fungal spores and decreased palatability of leaf litter. Production of fungal spores follows a very strong annual cycle connected with the periodicity of external conditions (Ingold 1971). It usually peaks in late summer and fall. Rastin et al. (1990) found that fruiting-body formation by litter-decomposing fungi in a spruce forest floor began in July, biomass production remained low during the summer months, increased considerably in fall, and reached its maximum in October and November. Based on both field and laboratory work, Knight & Angel (1967) believed that fungal spores were preferred over all other food types by *Tomocerus flavescens*, and that the low spore content in field animals was due to lack of spores in the field. The field animals they analyzed were collected between mid-June and

mid-August, and the present study also showed relatively low fungal spore content during this period.

Newly fallen leaves are not a preferred food for most soil animals; they must be conditioned for some time before the animals will ingest them (Seastedt 1984). It has been demonstrated that the longer leaves have been on the ground, the higher the rate at which they will be consumed by Collembola (Sadaka & Poinot-Balaguer 1987a and b, 1989; Sadaka et al. 1988). Schaller (1949) also indicated that Collembola would not feed on fresh leaves. In the study sites, peak abscission occurred during September and October (Snider & Snider 1989, 1991). These freshly fallen leaves would not serve as a food source for surface-dwelling *O. hexfasciata* and *S. henshawi*.

There could be two possible reasons for the appearance of plant materials in the guts of *S. henshawi* and *O. hexfasciata*: 1) when the animals feed on fungi, they accidentally ingest the plant materials connected with fungi; 2) plant materials serve as secondary food source when fungal spores become scarce, providing some nutrition.

Fungal spores found in these three species consisted of a large number of species. Different fungal species have been related to different decomposition stages of leaf litter and to leaf litter species (Kendrick & Burges 1962; Hudson 1968; Widden & Parkinson 1973). In food preference experiments, it has been demonstrated that Collembola selected some fungal species over others. Unfortunately, identification of fungal species found in collembolan guts was beyond the scope of this study.

Pollen has been shown to be a highly valuable food for a large number of insects (Kevan & Kevan 1970). Although *Entomobrya comparata* Folsom was observed on the pollen cones of pine trees during their flowering season, there was no evidence of *O. hexfasciata* visiting pollen cones to feed on them. Pine pollen matures only in May and June and is wind-disseminated in great abundance (Barnes & Wagner 1981). The availability of pine pollen is thus seasonal, as is its appearance in the collembolan diet from May to June of each year. Pollen probably plays an important role in the nutrition of these Collembola, especially of *O. hexfasciata* during spring.

Scott & Stojanovich (1963) found intact juniper pollen in the gut of *Onychiurus pseudo-fimetarius* Folsom in various stages of digestion. Both intact and broken pine pollen were also observed in the gut of *O. hexfasciata*, intact pollen measuring about $80 \times 40 \mu\text{m}$. It was clearly indicated that *O. hexfasciata* "swallows" these foods instead of chewing them before ingestion.

There were pine trees in the area surrounding both sites, but not in the sites themselves. Dissemination distance of pine pollen is affected by environmental conditions. High humidity during dissemination would limit the distance pollen can travel. The difference in percent of pollen in *O. hexfasciata* guts between 1988 and 1990 could be related to the amount of rainfall during dissemination. The year 1988 was a very dry year, and significant rains did not begin until the end of the first week of August (Snider & Snider 1989). There could have been more pollen distributed over both sites in the drought year of 1988 than in the relatively wet year of 1990. Pollen was thus likely to be more available to collembolans in 1988 than in 1990, and gut content analysis showed a high pollen content in 1988.

The three collembolan species living in or on the forest floor probably occupied different microhabitats. It has long been realized that Collembola are morphologically adapted to a greater or lesser degree to either a subterranean or surface-dwelling mode of life (Poole 1961). Species with pigment distributed in patterns; 8 + 8 large eyes; strong furcula; long antennae, legs and setae; complicated sensory setae on the tibiotarsi; and lack of postantennal organ are considered epigeic forms (including most entomobryids and sminthurids). *Sminthurinus henshawi* can be found in above-ground habitats (Snider, personal communication). On the other hand, *I. notabilis* represents the transitional form from hemiedaphic to euedaphic, being absent from above-ground habitats, and dwelling mainly in litter and humus layers (Bockemühl 1956; Poole 1961). In the present study, *I. notabilis* frequented both leaf litter and A horizon, whereas the other

two species, *S. henshawi* and *O. hexfasciata*, were clearly surface-dwelling and did not frequent soil.

In summary, these data suggest that size as well as type of food particles consumed are important in niche segregation of litter-dwelling Collembola. In two similar but spatially separated forests, each collembolan species foraged on very similar foods, in terms of food type as well as particle size. Species-specific mouthpart morphology determined the particle size ingested. Gut contents of each species also reflected seasonal variations in available food type and the influence of environmental conditions. All together, these observations document mechanisms for reducing interspecific competition for food among species occupying the forest floor.

References

- Anderson, J. M., Healey, I. N. (1972) Seasonal and inter-specific variation in major components of the gut contents of some woodland Collembola. *J. Anim. Ecol.* **41**, 359–368.
- Barnes, B. V., Wagner, W. H., Jr. (1981) Michigan trees. Univ. Mich. Press, Ann Arbor, MI. 384 pp.
- Bockemühl, J. (1956) Die Apterygoten des Spitzberges, eine faunistisch-ökologische Untersuchung. *Zool. Jb., Syst.*, Jena **84**, 113–194.
- Bödvarsson, H. (1970) Alimentary studies of seven common soil inhabiting Collembola of southern Sweden. *Ent. Scand.* **1**, 74–80.
- Borror, D. J., De Long, D. M., Triplehorn, C. A. (1976) An introduction to the study of insects. Holt, Rinehart and Winston, New York, p. 738.
- Chen, B., Snider, R. J., Snider, R. M. (in press) On the mouthpart structure of some Collembola. (*Inverteb. Biol.*).
- Christian, E. (1989) Biogeography, substrate preference, and feeding types of North Adriatic intertidal Collembola. *Marine Ecol.* **10**, 79–94.
- Cummins, K. W. (1973) Trophic relations of aquatic insects. *Ann. Rev. Entomol.* **18**, 183–206.
- Fjellberg, A. (1985) Recent advances and future needs in the study of Collembola biology and systematics. *Quaest. Ent.* **21**, 559–570.
- Gilmore, S. K., Raffensperger, E. M. (1970) Foods ingested by *Tomocerus* spp. (Collembola, Entomobryidae), in relation to habitat. *Pedobiologia* **10**, 135–140.
- Goto, H. E. (1972) On the structure and function of the mouthparts of the soil-inhabiting collembolan *Folsomia candida*. *Biol. J. Linn. Soc.* **4**, 147–168.
- Harbach, R. E. (1977) Comparative and functional morphology of the mandibles of some fourth stage mosquito larvae (Diptera: Culicidae). *Zoomorphologie* **87**, 217–236.
- Hudson, H. (1968) The ecology of fungi on plant remains above the soil. *New Phytologist* **67**, 837–874.
- Ingold, C. T. (1971) Fungal spores: their liberation and dispersal. Oxford Univ. Press, Oxford, 302 pp.
- Joosse, E. N. G., Testerink, E. J. (1977) The role of food in the population dynamics of *Orchesella cincta* (Linné) (Collembola). *Oecologia* **29**, 189–204.
- Kaneko, N. (1988) Feeding habits and cheliceral size of oribatid mites in cool temperate forest soils in Japan. *Rev. Ecol. Biol. Sol* **25**, 353–363.
- Kendrick, W. B., Burges, A. (1962) Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova Hedwigia* **4**, 313–342.
- Kevan, P. G., McE. Kevan, D. K. (1970) Collembola as pollen feeders and flower visitors with observations from the high Arctic. *Quaest. Entomol.* **6**, 311–326.
- Knight, C. B., Angel, R. A. (1967) A preliminary study of the dietary requirements of *Tomocerus* (Collembola). *Amer. Midland Natur.* **77**, 510–516.
- Knight, C. B. (1976) Seasonal and microstratal dietary research on *Tomocerus* (Collembola) in two forested ecosystems of eastern North Carolina. *Rev. Ecol. Biol. Sol* **13**, 595–610.
- Manton, S. M. (1964) Mandibular mechanisms and the evolution of arthropods. *Phil. Trans. R. Soc.* **247**, 1–183.
- McMillan, J. H. (1975) Interspecific and seasonal analyses of the gut contents of three Collembola (Family Onychiuridae). *Rev. Ecol. Biol. Sol* **12**, 449–457.
- Poole, T. B. (1959) Studies on the food of Collembola in a douglas fir plantation. *Proc. Zool. Soc. London* **132**, 71–82.
- Poole, T. B. (1961) An ecological study of the Collembola in a coniferous forest soil. *Pedobiologia* **1**, 113–137.

- Rastin, N., Schlechte, G., Hüttermann, A., Rosenplänter, K. (1990) Seasonal fluctuation of some biological and biochemical soil factors and their dependence on certain soil factors on the upper and lower slope of a spruce forest. *Soil Biol. Biochem.* **22**, 1049–1061.
- Sadaka, N., Poinso-Balaguer, N. (1987a) Relations trophiques entre le collembole *Onychiurus zschokkei* Handschin et les feuilles de chêne vert *Quercus ilex* L., a divers stades de décomposition. *Rev. Ecol. Biol. Sol* **24**, 329–340.
- Sadaka, N., Poinso-Balaguer, N. (1987b) Determination of amino acids in leaves of evergreen oak at four different stages of decomposition. *Biol. Fert. Soils* **5**, 158–163.
- Sadaka, N., Poinso-Balaguer, N. (1989) Relations trophiques feuilles de chene vert (*Quercus ilex* L.) – Collemboles. Influence de la qualité du matériel foliaire sur la croissance pondérale d'*Onychiurus zschokkei* Handschin. *Rev. Ecol. Biol. Sol* **26**, 197–204.
- Sadaka, N., Poinso-Balaguer, N., Talin, J. (1988) Relations trophiques feuilles de chêne vert (*Quercus ilex* L.) – Collemboles. Influence de la qualité du matériel foliaire sur la biologie d'*Onychiurus zschokkei* Handschin et *Folsomia candida* Willm. *Vie et milieu* **39**, 33–39.
- Schaller, F. (1949) Biologische Beobachtungen an humusbildenden Bodentieren insbesondere an Collembolen. *Zool. Jb. Abt. Syst.* **78**, 506–525.
- Scott, H. G., Stojanovich, C. J. (1963) Digestion of juniper pollen by Collembola. *Florida Entomologist* **46**, 189–191.
- Seastedt, T. R. (1984) The role of microarthropods in decomposition and mineralization processes. *Ann. Rev. Entomol.* **29**, 25–46.
- Snider, R. J., Snider, R. M. (1987) ELF ecological monitoring in Michigan. I. Description of sites for soil biological studies. *Pedobiologia* **30**, 241–250.
- Snider, R. J., Snider, R. M. (1989) ELF communications system ecological monitoring program: Arthropoda and earthworms. In: Compilation of 1988 annual reports of the Navy ELF communications system ecological monitoring program. Technical report E06595-6. Contract No. N00039-88-C-0065 Vol. 2, 72 pp.
- Snider, R. J., Snider, R. M. (1990) ELF communications system ecological monitoring program: Arthropoda and earthworms. In: Compilation of 1989 annual reports of the Navy ELF communications system ecological monitoring program. Technical report E06620-4. Contract No. N00039-88-C-0065 Vol. 2, 108 pp.
- Snider, R. J., Snider, R. M. (1991) ELF communications system ecological monitoring program: Arthropoda and earthworms. In: Compilation of 1990 annual reports of the Navy ELF communications system ecological monitoring program. Technical report E06628-4. Contract No. N00039-88-C-0065 Vol. 2, 128 pp.
- Snider, R. J., Snider, R. M. (1992) ELF communications system ecological monitoring program: Arthropoda and earthworms. In: Compilation of 1991 annual reports of the Navy ELF communications system ecological monitoring program. Technical report E06200-2. Contract No. N00039-88-C-0065 Vol. 2, 65 pp.
- Surtees, G. (1959) Functional and morphological adaptations of the larval mouthparts in the sub-family Culicinae (Diptera) with a review of some related studies by Montschadsky. *Proc. R. Ent. Soc. Lond. (A)* **34**, 7–16.
- Takeda, H., Ichimura, T. (1983) Feeding attributes of four species of Collembola in a pine forest soil. *Pedobiologia* **25**, 373–381.
- Wallace, J. B. (1975) Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis*, *Cheumatopsyche etrona*, and *Macronema zebratum* (Hydropsychidae). *Ann. Entomol. Soc. Am.* **68**, 463–472.
- Wallace, J. B., Merritt, R. W. (1980) Filter-feeding ecology of aquatic insects. *Ann. Rev. Entomol.* **25**, 103–132.
- Widden, P., Parkinson, D. (1973) Fungi from Canadian coniferous forest soils. *Can. J. Bot.* **51**, 2275–2290.